第24卷 第4期　　古脊椎动物学报　　Vol. XXIV, No. 4
1986年10月　　VERTEBRATA PALASIATICA　　Oct., 1986

禄丰古猿地点的树鼩类化石

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关键词　云南禄丰　最晚中新世　石灰坝组　攀鼩目

内　容　提　要

本文记述的一种树鼩 *Prodendrogale yunnanica* gen. et sp. nov. 系1983年采集于云南禄丰最晚中新世的石灰坝组。材料仅有十余枚牙齿，但代表了化石树鼩在印度-巴基斯坦次大陆西瓦立克系外的唯一发现。文中除对该树鼩的形态作了描述和对比外，还评述了西瓦立克系发现的树鼩化石，同时对树鼩类的系统发育作了一些探讨。

树鼩系一类善攀援、外形似松鼠的小哺乳动物，现生的种类仅分布于东洋界。由于它在构造、习性和行为上与原始的灵长类及食虫类都具有一些相似的特征，故其高阶元的归属，一直是个有争议的问题。许多学者认为，树鼩与灵长类有着特别的亲缘关系，认为它很可能与灵长类的起源有关。辛普生 (Simpson, 1945) 在其《哺乳动物分类原则及分类》一书中，还把树鼩归入了灵长目的狐猴次目 (Lemuriform)。但近二十多年来，随着分支系统学的理论和方法在生物系统学的传播和应用，也使评估树鼩亲缘性的注意力集中在对其系统发育关系的分析。其结果使许多学者相信，树鼩并不属于灵长类。W.P. 勒基特 (Luckett, 1980) 所编著的《Comparative Biology and Evolutionary Relationships of Tree Shrews》一书，正充分反映了这一观点。通过对树鼩和低等灵长类头骨、齿系、神经和生殖系统等的性状研究，书中的学者认为，树鼩与低等灵长类的某些相似，只不过是近祖共性或系趋同进化的结果；它所独有的衍生性状，无一可包含于灵长目这一单系中。因此认为，树鼩既不属于食虫目，也不可划入灵长目，而自身构成一个独立的单系。这样，华格纳 Wagner (1855) 把它另立一目——攀鼩目 (Scandentia) 的主张得到越来越多学者的赞同 (见 Butler, 1972)。本文作者不打算详细讨论这些问题，但采纳了把树鼩归入攀鼩目的这一意见。

所记述的材料，仅有一些单个的牙齿，标本系1983年从云南禄丰古猿地点D剖面中筛洗而得。(关于化石地点的地质概况，详见祁国琴，1985，禄丰古猿化石地点地层概述一文)。牙齿的特征在树鼩科内作属、种的区分意义颇大，莱昂 (Lyon, 1913)，斯蒂尔 (Steele, 1973) 和巴特勒 (Butler, 1980) 对现生树鼩的齿系作过较详细的研究，乔普拉等 (Chopra et al., 1979, 1979) 和雅各布斯 (Jacobs, 1980) 等亦对西瓦立克化石树鼩的牙齿作过很好的描述。本文描述牙齿构造的术语，即采用了巴特勒 (1980) 的命名，同时参考了哈奇森 (Hutchison, 1974) 描述鼹鼠时使用的部分术语。

蒙邱占祥、李传夔、王应祥和吴文裕等同志阅读和修改文稿，承沈文龙同志绘图、欧阳莲同志作扫描摄像，作者在此一并致谢。

攀鼩目 Scandentia Wagner, 1855
树鼩科 Tupaiidae Mivart, 1868
原细尾鼩属(新属) *Prodendrogale* gen. nov.

属名称由来　前缀"Pro"意为在前，示新属与细尾鼩属 *Dendrogale* 近似，但较原始。

属型种　*Prodendrogale yunnanica* sp. nov.

属的特征　牙齿的大小和形态接近于 *Dendrogale* 者。但 C^1 双根融合；P^3 和 P^4 的前附尖弱；M^{1-2} 具较发育的外齿带；M^2(M^1 也可能)具前小尖；P_4 相对较大，但下后尖较低弱，下前尖位置靠中；M_{1-2} 具明显的前唇侧齿带。

云南原细尾鼩(新种) *Prodendrogale yunnanica* gen. et sp. nov.

(图版 I；图 1-3)

1985: Tupaiidae gen. et sp. indet.，邱铸鼎等，人类学学报，*4*(*1*)：*13-32*。

种名称来由　示新种之产地——云南省

特征　同属特征

正型标本　一右 M^2，其后外谷部分破损（中国科学院古脊椎动物与古人类研究所编号：V8281）。

模式产地　云南省禄丰县石灰坝。

时代与层位　最晚中新世，保德期；石灰坝组(D 剖面第 5 层)。

归入标本

第 1 层：右 P^2，破右 M^1，左 M_3 后跟各一枚 (V8282.1—3，依顺序，下同)；

第 2 层：左 DP^3，破左 P^3，破右 I_1 及 M_1 的后跟各一枚 (V8282.4—7)；

第 5 层：一破右 P^3，一破左 P^4，一右 M^3，一破左 I_2，一右 M_1 及一左 M_2(V8282.8—13)；第 6 层：右 C^1，右 DI_1，及左 P_4 各一枚 (V8282.14—16)。

测量(单位：毫米)

标本数	C^1	P^2	P^3	P^4	M^1	M^2	M^3	P_4	M_1		M_2		M_3	
	1	1	2	1	1	1	1	1	2		1		1	
长	1.25	1.25	1.68*	1.75	2.50	2.25	1.50	1.90	2.45		2.40		—	
宽	0.60	0.58	—	—	—	2.60	2.60	1.25	tri. 1.40	tal. 1.60	tri. 1.40	tal. 1.35	tri. —	tal. 1.15

* 平均值

描述　上犬齿(C^1)前臼齿化，具两融合的齿根。齿冠锐利，扁锥形。主尖有一长的后脊和一稍短的前脊，两脊在牙齿基部略膨大。

P^2 的形状大体与 C^1 相似，但两齿根分开，主尖不甚锐利，后脊较强大，并与一显著的后基尖连接。前脊不发育，牙齿的前方有一极弱的小尖。

P^3 比 P^2 大得多，相当臼齿化。主尖（前尖）高大，有一伸向齿冠后外角的粗壮齿脊，脊的舌侧壁陡峻，唇侧凹陷成窝。无后尖。齿带在牙齿后外角相当发育，但唇侧齿带向前未逾越前尖。主尖的前外角有一小的前附尖，前附尖与主尖的基部间有一弱脊。前舌侧亦有一齿带，与后齿带相比，它显得很弱。两枚 P^3 的原尖架 (Protocone shelf) 都已破损。该齿具三根。

P^4 的原尖架亦损失。从可比较的部分看，P^4 与 P^3 十分相似：主尖大，前外侧有一低的前附尖，后侧有一伸达牙齿后外角的强脊；没有后尖；牙齿的后唇侧具连续而发育的齿带。但 P^4 似较 P^3 横宽；前尖与前附尖间的脊较明显；主尖的唇侧不突起，因而牙齿的外侧形成很大的凹谷；外齿带连续，前舌侧齿带也较发育。P^4亦具三根。

M^1 只有牙齿的外半部分。前尖和后尖呈V形，前者比后者小而低。前嵴 (paracrista) 最短，与前附尖连接；后嵴 (metacrista) 最长，伸达牙齿的后外角；无后附尖；后前嵴和前后嵴连接于中附尖。中附尖比前附尖稍大，从唇侧壁的弯凹推断，中附尖由两小尖组成。前尖与后尖间的沟开阔，外伸唇侧；深度大，与浅的外谷 (ectoflexus) 对照鲜明。唇侧有一脊状的齿带，齿带从前附尖伸向中附尖，终止于后嵴末端，并几乎封闭外谷。M^1 的唇侧具两齿根。

M^2（图 1）的后外谷部分破损。牙齿轻微磨蚀。其外侧的尖、脊之形态和构造与M^1者无大异，唯前尖和后尖的大小差异不如 M^1 的那么明显；中附尖未见分成两小尖；前附尖位置较靠唇侧，因而从前尖和后尖向唇侧伸出的两臂较为匀称。与 M^1 相比，前嵴相对后前嵴要长些，后嵴不那样强壮，那样明显地掠向后外；外谷的齿带似乎也弱些。M^2 的原尖架约占牙齿宽度之半。原尖V形，位于齿冠前半部；其前臂沿牙齿的前缘往前外伸，并作为前尖前缘一狭窄的齿带直达前附尖；后臂沿牙齿的后缘向后外伸，消失于后尖基部的后舌侧。前臂在接近前尖处膨大成一触目的前小尖。牙齿的舌侧壁光滑，无齿带及次尖的痕迹。M^2 三根。

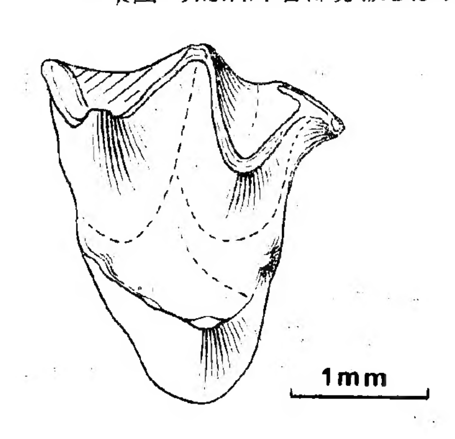


图 1 云南原细尾鼩（新属、新种），右 M^2，正型标本 (V8281)，冠面视

Fig. 1 *Prodendrogale yunnanica* gen. et sp. nov., right M^2, type (V8281), occlusal view

M^3 的后外角很退化，因而齿冠呈三角形。前尖最高。前嵴长，但无后嵴。前附尖发育，向牙齿的前外侧扩伸。中附尖仍相当大，由两小尖组成。后外谷较深，无后外齿带。原尖架与 M^2 者相仿，仅尺寸较小，其上的前小尖较模糊。M^3 三根，后唇侧根与舌侧根靠近。

标本中的 I_1 齿尖已破损，齿根亦未保存。其舌面的两侧各有一终止于牙齿基部的脊。舌面隆起成强大的中间嵴。

I_2 破碎。构造无异于 *Tupaia* 和 *Dendrogale* 者。不同于 I_1 在于个体较大；为中间嵴分成的两小面的夹角较大；可能齿尖部分也较宽阔。

P_4 保存良好。齿座臼齿化，三齿尖近直角三角形排列。齿座角 (trigonid angle) 开

口大。下后尖显著，完全独立于下原尖，位于唇侧比下原尖稍靠后的位置上。下原尖粗大，比下后尖也高得多。下前尖最低，但相当发育，位置很靠舌侧。后跟极弱，斜向唇侧，沿其内缘和后缘发育一脊，该脊在牙齿的后内角逐渐加厚成齿尖状突起。后跟的中间尚有一小的纵向嵴。P_4 双根。

材料中有形态十分相似的两枚下臼齿。其中 V8282.12 标本的下前尖及下内尖虽已破损，但根据齿座的前部较窄及斜脊会于齿座之中部偏唇侧判断，它很可能为 M_1；V8282.13 标本保存良好（图 2），根据其齿座和跟座近等宽，斜脊会于齿座后侧之正中部，无疑应为 M_2。两臼齿的齿座与 P_4 的很相似，只是前者的下前尖及下后尖相对较发育，下后尖比下原尖仅略低，齿座角开口小。未磨蚀的 M_1 跟座（V8282.7）表明，下内尖几乎与下次尖等高，后者为跟座中最大的齿尖。跟座上的尖比下原尖和下后尖都低。下内尖前方有一下内尖嵴（entocristid），但无下内小尖（entoconulid），也没有明显的下后尖嵴（metacristid）。下次小尖低而小，位于下内尖后方略偏唇侧的位置上，以一粗壮的下次脊连接于下次尖，与下内尖则以一深沟隔开。跟凹比齿凹宽大，而且位置明显较低。M_1 和 M_2 的前唇侧缘都有一明显的齿带，V8282.13 标本的后缘具齿带的模糊痕迹。M_1 和 M_2 都具两强大的齿根。

代表 M_3 的仅有一跟座。其形态和构造无异于 M_1 和 M_2 者，但较为狭小，齿尖亦较退化。

DP³ 三角形，比 P³ 小。其外侧部与 P³ 相应部分构造相似，唯前附尖较弱，后内侧齿带缺失。牙齿的内侧部薄弱，其上有一清楚，但很低小的原尖。DP³ 同样有分离的三齿根。

A

1mm

B

图 2　云南原细尾鼩（新属、新种），左 M_2（V8282.13）。A，冠面视；B，舌侧视

Fig. 2　*Prodendrogale yunnanica* gen. et sp. nov., left M_2 (V8282.13). A, occlusal view; B, lingual view

DI_1 除个体较小外（长 1.75mm），无异于 I_1。

比较与讨论　树鼩的化石非常罕见。本世纪初报道过一些早第三纪的"树鼩"，或者认为是与树鼩有亲缘关系的一些属，但先后都一一被否定了。在东亚，有马修和葛兰杰（Matthew et Granger, 1924）作为树鼩类描述的蒙古渐新世三达河组（Hsanda Gol）和洛层（Loh）的 *Tupaiodon*，后被辛普生（Simpson, 1931）归入了蝟类。辛氏（1931）记述的蒙古渐新世乌兰戈察组（Ulan Gochu）的 *Anagale gobiensis* 及步林（Bohlin, 1951）描述的甘肃渐新世的 *Anagalopsis kansuensis*，都一度被认为属树鼩，但麦克纳（Mckenna, 1963）根据耳区的研究，又都排除了它们属于树鼩类的可能。在北美，所有原先作为"树鼩"描述的 *Entomolestes*, *Leipsanolestes* 和 *Eudaemonema* 等，也都先后被重新订正（详见 Krishtalka, 1976; Krishtalka and West, 1977 和 Van Valen, 1965）。

目前公认确实为树鼩类的化石在国外仅发现于印巴次大陆的中新统。有乔普拉等(Chopra et al., 1979) 报道的印度喜马偕尔邦中西瓦立克系的一具右 M^{1-3} 的破碎头骨 (PUA I-5) 及一右 M_2(PUA I-6);乔普拉和瓦西沙特 (Chopra and Vasishat, 1979)记述的上述地点附近,同一层位,保存较好的一件头骨 (PUA I-3); 以及雅各布斯 (Jacobs, 1980) 描述的巴基斯坦中西瓦立克系一件未保存牙齿的破碎头骨 (YGSP 8089) 和一枚可能为左 M_1 的单个牙齿 (YGSP 8090)。

把禄丰标本归入树鼩,是因为其下门齿有一非常隆起的纵向嵴,此嵴把舌侧面分成两近于垂直的小面;上前臼齿,尤其是 P^3 和 P^4 的后唇侧凹陷,并有一明显的后外齿带;P_4 的齿座高度臼齿化;上臼齿外谷的位置明显较齿凹高,且唇侧具发育的齿带;下臼齿齿凹与跟凹的位置也高低悬殊,次小尖靠近下内尖,其间有一深沟. 当然,这些特征并不都为树鼩所独具,其中的一些性状也并非存在于所有的树鼩。在一些食虫类,甚至低等灵长类中,也有相似的牙齿构造,但是,这些标本所具有的组合特征,除树鼩外,无一可与其比较。而且,P^3 和 P^4 有一唇侧齿带围成的凹谷; 高度臼齿化的 P_4 具特别向唇侧倾斜的后跟;上臼齿由发育的齿带封闭的外谷位置明显比齿凹高; 下臼齿齿凹位置也比跟凹高很多的这些性状,则为树鼩类的牙齿所特有。

乔普拉和瓦沙特(1979)在研究印度的化石树鼩时, 把所发现的上述三件标本都指定为树鼩科的一新属 *Palaeotupaia*,认为该属在形态和构造上与现生 *Tupaia* 的最为接近,并认为巴基斯坦的两件标本亦可能属于该新的分类单元。*Palaeotupaia sivalicus* 的正型标本(PUA I-3) 在形态上确实与 *Tupaia* 很接近,或许表明了它们有较近的亲缘关系。但是,如把印度次大陆的这些化石都归入同一属、种,则很值得商榷。据描述, PUA I-5 标本的 M^{1-2} 方形,具次尖,而 PUA I-3 的 M^{1-2} 呈三角形,没有次尖。PUA I-3 在大小上虽与巴基斯坦的 YGSP 8089 接近,但印度标本的 C^1 和 P^2 都为单根,而后者均为双根。PUA I-6 有发育的前齿带, 而 YGSP 8090 却完全缺失。依现生树鼩标本的观察, 臼齿次尖的有无,C^1 的齿根数及臼齿的齿带发育与否, 都是树鼩科中区别属、种的重要特征。因此,在笔者看来,印巴次大陆发现的材料,至少代表了三种化石树鼩。

禄丰标本不同于印度标本在于上臼齿没有后附尖,又以没有次尖而异于其中的 PUA I-5 标本, 以 C^1 及 P^2 具双根而不同于 PUA I-3。虽然禄丰标本的 M_2 与印度标本的同一牙齿 (PUA I-6) 都有前唇侧齿带,但后者的个体较大, 且跟座似乎比齿座明显宽。由于巴基斯坦 YGSP 8089 标本的齿冠未保存,无法与禄丰标本作齿冠构造上的比较。虽然它们的 C^1 和 P^2 齿根数目相同,但我国标本的牙齿个体要小得多。YGSP 8090 的大小及形态与禄丰标本的下臼齿都很相近,但巴基斯坦的 M_1 没有前齿带。显然,禄丰化石树鼩所具有的特征,与印巴次大陆的标本都有较大的差异。

莱昂 (Lyon, 1913) 最早对树鼩科的现生属、种进行了描述和划分。根据外部形态、头骨、齿系及生活习性等,莱氏把现生的树鼩分成两亚科: 树鼩亚科 (Tupaiinae) 和羽尾亚科 (Ptilocercinae)。前一亚科包括了五个属: *Tupaia*, *Anathana*, *Dendrogale*, *Lyonogale* 及 *Urogale*; 后一亚科仅有 *Ptilocercus* 一属。 这一划分几乎为所有学者所接受, 只是由于 *Dendrogale* 在形态和构造上具有较多的原始性状,并显示了一些介于羽尾亚科和树鼩亚科的特征, 因而戴维斯 (Davis, 1938) 曾对这两亚科的有效性表示怀疑, 但 Luckett

(1980) 认为，戴氏所引证 *Dendrogale* 与 *Ptilocercus* 的相似特征，大多系树鼩类的近祖共性，而 *Dendrogale* 与 *tupaiids* 的相似都表现为近裔共性，从而从系统发育关系上进一步肯定了把树鼩类分成两亚科的合理性。

云南化石树鼩在牙齿大小上与 *Ptilocercus* 接近，而且 C^1 也具有双根，但羽尾树鼩的上臼齿没有中附尖，上、下臼齿外侧都有发达和连续的齿带，这便排除了禄丰标本属于 Ptilocercinae 亚科的可能。Tupaiinae 中的 *Anthana*, *Lyonogale* 和 *Urogale* 属的个体较大，C^1 单根，上臼齿都有或具很发育的次尖。 此外，*Anthana* 的臼齿短宽，*Lyonogale* 的 C^1 无明显的后脊，*Urogale* 的中附尖为一脊状构造。因此，禄丰的标本也不可能归入树鼩亚科的上述三属。 就牙齿的大小而言，它与 *Dendrogale* 及 *Tupaia* 属中的个体最小者 *T. minor* 接近，只是其 C^1 具双根，上臼齿又无任何次尖的痕迹，使它较相似于前者，有别于 *T. minor*。

Dendrogale 分布于印支半岛的东南部和加里曼丹。该属仅有 *D. murina* 和 *D. melanura* 两种(见 Lekagul et Muneely, 1977) 据莱昂描述，这两种在牙齿的形态和构造上难于区别。禄丰标本与 *D. melanura* 齿系的比较表明：两者牙齿大小接近，在 C^1 双齿根和上臼齿无次尖方面相同，其它的一些特征也都相似，如 C^1 明显比 P^2 大，有一发育的后脊，P^2 的双根分开，有一后脊及弱的后基尖，P^3 比 P^2 大很多，并有一前附尖，M^1 的中附尖由两小尖组成，M^2 的后尖明显比前尖高，下臼齿下后尖的位置较下原尖靠后，且前者比后者低，M_2 跟座与齿座等宽，下内尖较下次尖低等。但是，在牙齿的特征上， 禄丰树鼩依然易于与 *Dendrogale* 相区别：前者 C^1 的双根融合，其前齿带没有后者的那样明显，P^2 有一弱的前基尖和一较强的后脊，且相对于 C^1 要比 *Dendrogale* 的大，P^3 和 P^4 的前附尖弱，M^{1-2} 的外齿带较发育，M^2(M^1 也可能)有一前小尖，M^3 中附尖分成双尖，P_4 的下原尖比下后尖高很多，下前尖较靠舌侧，下臼齿前唇侧缘具明显的齿带。

从上述的比较看来，禄丰的树鼩标本虽然只有一些单个的牙齿，但其特征充分表明了该化石树鼩不仅不同于印度次大陆中新世的树鼩，也与现生的各属有所差异。 虽然与 *Dendrogale* 在牙齿形态上较接近，但考虑到地史上的时间差距，这里只把它当作树鼩科中与 *Dendrogale* 属很接近的一新的属、种 *Prodendrogale yunnanica*。

新属与 *Dendrogale* 形态上的相似，表明了它们有较接近的亲缘关系。在许多方面，它又具有比现生属明显原始的特征，可能说明它们具有祖裔的亲缘关系。在 *Prodendrogale-Dendrogale* 的这一支系中，牙齿的进化趋势似乎表现于 C^1 前齿带的出现，P^2 的退化(个体缩小，失去弱的后尖，后脊变弱)，P^3 和 P^4 前附尖的增大，M^{1-2} 外齿带的退化，P_4 个体的缩小，其下后尖的增高和下前尖的外移，M_{1-2} 前唇侧齿带的退化等。

Prodendrogale 似乎又具有在系统发育上的一些进步特征，如 C^1 双根融合，M^2 具前小尖，M^3 中附尖分开等。根据与外类群的比较，特别是对双脊齿型 (*dilambdodent*)。哺乳动物牙齿系统发育的研究（参见 Butler, 1980)，这里把树鼩类 C^1 的单根和中附尖的分开当作衍生的特征。因此，如果 *Dendrogale* C^1 双根的分开和 M^3 中附尖的双尖不是一种次生现象，以及上臼齿前小尖的出现是一种衍生性状的假说是正确的话，那么在系统发育上，*Prodendrogale* 与 *Dendrogale* 则构造了一姐妹群．两者的 C^1 都具双根，这无疑属近祖共性．它们又共有臼齿失去次尖这一近裔性状，因此，这一单系可能与具有 C^1 单根

这一衍生性状的 *Tupaia* 和 *Lyonogale* 有更接近的亲缘关系，并同时远离 Ptilocercinae 亚科，从上臼齿具有中附尖及下臼齿次小尖靠舌侧的共同祖先，向着次尖退化方向进化。至于印度的 *Palaeotupaia sivalicus*（仅指正型标本），没有次尖，但具有 C^1 单根，P^3 原尖发育，臼齿具后附尖的这些近裔性状，可能表明了它与现生 *Tupaia* 属在系统发育的关系上更为接近。图3 为新属在 Tupaiinae 亚科中的可能系统发育关系。

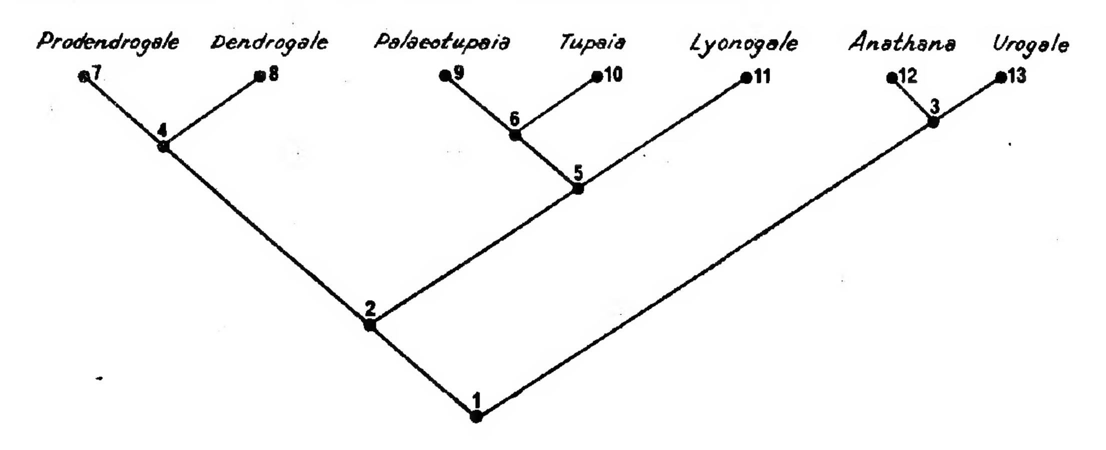


图 3 树鼩科各属的可能系统发育关系

说明：1.上臼齿具中附尖，下臼齿下次尖靠舌侧，C^1 双根；2.上臼齿次尖退化；3.上臼齿次尖加大，C^1 单根；4.上臼齿失去次尖；5.C^1 单根；6.上臼齿次尖极弱或无；7.C^1 双根融合，M^2 具前小尖；8.P^2 具前基尖，P_4 下后尖增高；9.P^3 原尖增大，上臼齿具后附尖；10.P^4 变窄；11.M^1_1 增长；12.上臼齿及下臼齿横向发育；13.C^1 加大，P_4 具次小尖.

Fig. 3 Distribution of selected apomorphic dental characters and possible phyletic relations of the genera of Tupaiidae

顺便提一下，在云南地区，现生的树鼩仅有 *Tupaia* 一属，该属只能与印度的 *Palaeotupaia* 而不会与我国的 *Prodendrogale* 有更接近的亲缘关系。与 *Prodendrogale* 有密切关系的现生 *Dendrogale* 的地理分布显然比禄丰地区靠南了许多，这与禄丰动物群 *Alilepus longisinuosus* 有一定关系的现生的 *Nesolagus* 分布于苏门答腊可能不是偶然的巧合，或许是表明禄丰当时的自然气候和生态环境与今日南亚靠南部较为接近。

（1986 年 3 月 11 日收稿）

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FOSSIL TUPAIID FROM THE HOMINOID LOCALITY OF LUFENG, YUNNAN

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Key words　Yunnan; Miocene; Tupaiidae

Summary

The present paper deals with a new Miocene tupaiid, *Prodendrogale yunnanica* gen. et sp. nov., which is the only record of fossil tree shrew outside the India-Pakistan subcontinent. The material was collected in 1983 by wet-sieving techniques from the deposits of Section D (see Qi, 1985) at the hominoid locality of Lufeng. Based on 17 isolated teeth, descriptions and comparison of the new taxon are made. The possible phyletic relations of the Lufeng tupaiid to other known genera of Tupaiidae are discussed in this paper as well.

Scandentia Wagner, 1855

Tupaiidae Mivart, 1868

Prodendrogale gen. nov.

Derivation Nominis Alludes to the similarities and primitiveness of the new genus to *Dendrogale.*

Diagnosis Close to *Dendrogale* in size and morphology, but C^1 with double united roots, P^3 and P^4 with rather weak parastyle, M^1 and M^2 with quite well developed labial cingulum, M^2 (probably also M^1) with paraconule, P_4 relative large with poorer developed metaconid and rather lingual displacement of paraconid, and M_{1-2} with distinct precingulum.

Prodendrogale yunnanica sp. nov.

(pl. I; fig. 1, 2, 3)

Etymology After Yunnan, the type locality of the new species.

Diagnosis As for the genus.

Type Locality Shihuiba, Lufeng, Yunnan.

Type Level Baodian, Uppermost Miocene.

Type A right M^2 (post ectoflexus damaged) (IVPP no. V 8281).

Descriptions The upper canine is a flat awl-like tooth with two united roots. Its main cusp has a long posterior and a short anterior crest. The two crests are somewhat swollen at the base of the crown, but no basal cusp is developed.

P^2 resembles C^1 in pattern, but its roots are disunited, its main cusp is less sharp and has a weak anterior cuspule and a stronger posterior crest leading to a posterior basal cusp.

The lingual shelf of the P^3 is damaged. The tooth is molarized and much larger than P^2. Its main cusp (paracone) has a strong crest extending to the posterobuccal corner of the crown. The lingual wall of the crest is steep, while the buccal is hollow. A crest joins the small parastyle to the base of the paracone. There is no metacone. The posterobuccal corner of the tooth is occupied by a continuous cingulum, but the cingulum does not extend past the paracone, P^3 has three separated roots.

The P^4 is only represented by a labial shelf. It is similar to that of P^3 in having the paracone as a dominant cusp, a low parastyle and strong posterior crest, and in having a well developed cingulum continuing the posterobuccal border of the tooth. The tooth, however seems to be transversally widened with a more developed anterolingual cingulum and a more broad labial flexus closed by a continuous buccal cingulum. P^4 is three rooted.

On M^1 the paracone and metacone are V-shaped cusps, the former being smaller and lower. The paracrista is short and connected with the parastyle, while the metacrista is long and extends to the posterobuccal corner. There is no metastyle, but a bifid mesostyle is present. The groove between the paracone and the metacone is striking and much deeper than the elevated ectoflexa. The ectoflexa are closed by a well developed labial cingulum. The protocone shelf of the M^1 is broken. There are two labial roots.

M^2 differs from M^1 in that: the paracone and metacone are subequal in size, separation of the mesostyle is less distinct, length of crista is more symmetrical, the parastyle points more buccally and there is a weaker posterobuccally cingulum. The protocone shelf of M^2 occupies about half of the width of the tooth. The protocone is also a V-shaped cusp with the anterior arm following the anterior edge of the tooth and leading as a cingulum past the paracone to join the parastyle, the posterior arm following the posterior border and disappearing at the posterolingual base of the metacone. Near the base of the paracone the anterior arm develops a

low paraconule. The anterior and posterior walls of the protocone are quite smooth and there is no trace of a hypocone. M^2 is three-rooted.

As is general in tree shrews, the crown of M^3 is triangular with a rather reduced postero-buccal corner. The paracone is much larger and higher than the metacone. The metacrista is absent, while the paracrista is the longest crests on the buccal shelf. The parastyle is well developed and points directly buccally. It is clear that the mesostyle is bifid. The protocone shelf is similar in morphology to that of M^2, but differs in size and absence of paraconule. M^3 has three roots.

The apex and root of the I_1 are not preserved. The tooth is flattened mesiodistally and its lingual surface is bounded by two enamel crests and a raised ridge divides the surface into two subequal facets, which are at right angles to each other.

I_2 differs from I_1 in being larger and having a larger angle of the two facets. It may also have a wider apex than I_2 does.

The trigonid of P_4 is molariform, with the protoconid being the dominant cusp. The metaconid is placed a little more posteriorly than the protoconid. It is lower and more subordinate relative to the protoconid than it is in living *Dendrogale*. The paraconid, the lowest cusp in the trigonid is situated rather lingually. The three trigonid cusps are arranged in an approximately right angle triangle. The trigonid angle is widely open. The talonid is simple. A crest follows the heel posterolingually, and develops a cuspule at the posterolingual corner of the tooth. P_4 is double-rooted.

Judged from the relatively wide anterior part of the trigonid and the oblique crest meeting the trigonid more buccally to the midline of the tooth, the molar V8282. 12 is considered as M_1. Its trigonid is similar to that of P_4, but the paraconid is more developed, the metaconid and protoconid are nearly equal in height, and the trigonid angle is not open so widely. The hypoconid is the largest cusp in the talonid. The entoconid has the same height as the hypoconid. The entoconid has a ectocristid running to the base of metaconid. There is no ectoconulid, nor metacristid. The hypoconulid, located a little less lingually posterior to the entoconid, is small and low. It is connected with the hypoconid by the strong hypolophid and separated from the entoconid by a groove. The talonid basin is larger than the trigonid basin, and the former is at a level distinct lower than the latter. There is a cingulum running below the paraconid antero-buccally. M_1 is two-rooted.

M_2 differs from M_1 in the anterior part of trigonid being narrower and the oblique crest joining the trigonid at the longitudinal midline of the tooth.

M_3 is only represented by a talonid, which is not differentiated from that of the first two molars morphologically except for its narrowness and reduced cusps.

DP^3 is triangular and smaller than P^3. Its labial shelf is similar to that of P^3, differs from it in having a weaker parastyle and absence of the posterolingual cingulum. The lingual shelf is poorly developed, on which stands a low, but a visible protocone. The tooth has also three separate roots.

DI_1 resembles I_1, but smaller (length: 1.75 mm).

Comparison and Discussion The specimens are reffered to the Tupaiidae because the possession of the following characters: a ridge is raised to divide lingual surface of the lower incisor into two subequal facets nearly at right angles; the buccal wall of upper premolars, especially P^3 and P^4 is hollow with a pronounced labial cingulum; the trigonid of P_4 is molariform; on M^1 and M^2 the ectoflexa are closed by a well developed labial cingulum and are at a

level much higher than the groove between the paracone and metacone; on M_1 and M_2 the trigonid basin does not extend below the level of the talonid one, and the hypoconulid is in a lingual position near and separated by a groove from the entoconid. An association of these characters distinguishes the specimens of tree shrew, although some of them are not unique to this animal or not present in all tupaiids.

Definitive records of fossil tree shrews include two cranial fragments (PUA 1—3, 4) and a M_2 (PUA 1—6) from the middle Siwaliks in India (see Chopra et al., 1979 and Chopra et Vasishat, 1979) and an anterior skull fragment without crowns of teeth (YGSP 8089) and a probably M_1 (YGSP 8090) from the Pakistan middle Siwaliks (Jacobs, 1980). Chopra and Vasishat (1979) assigned the specimens of India to a new genus *Palaeotupaia* and suspected that the specimens from Pakistan also belong to the same taxon. Their assignment, however, seems not to be confirmed by the differential features among the specimens mentioned above. The M^{1-2} are quadrate with a hypocone in the specimen no. PUA 1—5, while they are triangular without a hypocone in PUA 1—3. C^1 and P^2 in PUA 1—3 of India are single-rooted, but double in YGSP 8089 of Pakistan. In the lower teeth a prominent precingulum is present in PUA 1—6, but absent in YGSP 8090. It seems to me that specimens from the Siwaliks represent at least three taxa of tree shrews.

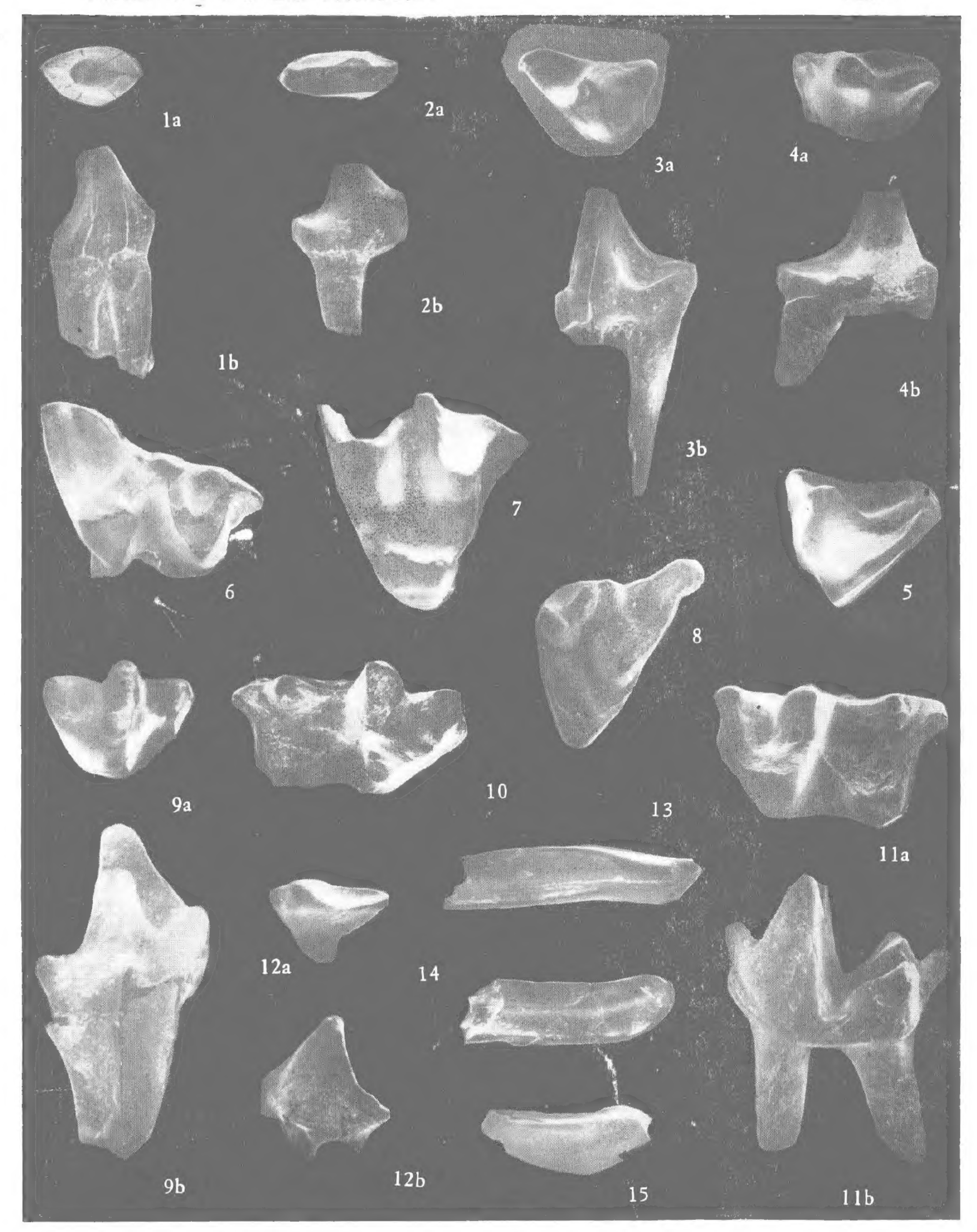
The specimens of Lufeng distinguish readily from those of India-Pakistan subcontinental: from the type of *Palaeotupaia sivalicus* (PUA 1—3) in having a double rooted C^1 and P^2; from PUA 1—5 in the absence of hypocone; from PUA 1—6 in M_2 having an equal width of trigonid and talonid; from YGSP 8089 by size and from YGSP 8090 by its presence of precingulum.

The Lufeng tree shrew is comparable to *Ptilocercus* in size and in having a double rooted C^1, but differs from the latter in the presence of mesostyle and the absence of continuous cingula on the buccal edge of the teeth. In the modern genera of the subfamily Tupaiinae it is similar to *Dendrogale* but distinct from *Anthana, Lyonogale, Urogale* and *Tupaia* in smaller size, in having a double-rooted C^1, and in the absence of hypocone. It is closer to *Dendrogale* than the others not only in size and in the two rooted C^1. but also in C^1 having a developed posterior crest larger than P^2, in the posterior crest of P^2 connected to the posterior basal cusp, the parastyle of P^3 much larger than P^2, the mesostyle of M^1 divided, the metacone of M^2 higher than the paracone, the talonid and trigonid of M_{1-2} equal width. Nevertheless, it can be differentiated from *Dendrogale* by its presence of two united roots in C^1, a faint anterior basal cusp and a more developed posterior crest on P^2, a weaker parastyle on P^3 and P^4, a developed labial cingulum on upper molars, a paraconule on M^2, a bifid mesostyle on M^3, a weaker and lower metaconid on P_4 and a well developed precingulum on M_1 and M_2.

Based on the characters mentioned above, the Lufeng Tupaiid is assigned to a new genus and species *Prodendrogale yunnanica* gen. et sp. nov. Some characters might suggest that *Prodendrogale* is an ancestor of *Dendrogale*. In the phyletic lineage *Prodendrogale-Dendrogale*, the evolutionary trend would be indicated by the presence of anterior cingulum on C^1, the reduction of P^2 (in size, lacking anterior cusp and weakening posterior loph), increase of parastyle on P^3 and P^4, reduction of labial cingula on upper molars, the development of metaconid and buccal location of paraconid on P_4, and the absence of precingulum on lower molars.

The new genus resembles *Dendrogale* in the double-rooted C^1, the absence of hypocone on upper molars. These are symplesiomorphies. It seems likely that the united root of C^1, the presence of paraconule on M^2 (probably also on M^1) and the bifucation of mesostyle on M^3 are of

derived characters. On the assumption that its differences to *Dendrogale* are apomorphic, the new genus may be regarded as a clade from the *Dendrogale* line in which the divergence of tooth has taken place independently. The two genera seem to have evolved from a common ancestor in losing the hypocone. Apparently, this monophyletical reduced hypocone, together with *Tupaia* and *Lybnogale,* initiated from an ancestral stage in which the hypocone resembled that of *Anathana* and *Urogale.* As to *Palaeotupaia* of India (type specimen only), its resemblance in the absence of hypocone to the new genus may be interpreted as plesiomorphy. It may be thought to be a clade with *Tupaia* in which the reduction of hypocone started from a stage of possession of a single root C^1. On the basis of the dendrogram given by Butler (1980), figure 3 is given to show the possible phyletic relations of *Prodendrogale* and *Palaeotupaia* to other known genera of Tupaiinae.



云南原细尾鼩(新属、新种) *Prodendrogale yunnanica* gen. et sp. nov.

1. C^1 dext. V8282.14; 2. P^2 dext. V8282.1; 3. P^3 dext. V8282.8; 4. P^3 sin. V8282.5; 5. P^4 sin. V8282.9; 6. M^1 dext. V8282.2; 7. M^2 dext. V8281, type; 8. M^3 dext. V8282.10; 9. P_4 sin. V8282.16; 10. M_1 dext. V8282.12; 11. M_2 sin. V8282.13; 12. DP^3 sin. V8282.4; 13. I_1 dext. V8282.6; 14. I_2 sin.V8282.11; 15. DI_1 dext. V8282.15. All occlusal view except for 1b,2b,9b,12b (lingual view) and 3b,4b,11b(labial view). X15